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BIOLOGICAL BULLETIN

STUDIES ON THE BIOLOGY OF PARACOPIDOSOMOPSIS.

III. MATURATION AND FERTILIZATION.1

J. T. PATTERSON.

INTRODUCTION.

In the second paper in this series (Patterson and Porter, '17) an account of the spermatogenesis was given. It was shown that males reared from unfertilized eggs carry the haploid number of chromosomes in their germ cells, and that as a consequence the first maturation division is abortive, while the second results in producing two equal spermatids, and hence two similar spermatozoa. The purpose of the present paper is to give an account of the maturation of the egg, and of fertilization.

It was originally planned to report on the maturation process both in fertilized and unfertilized eggs, but my series of the latter has proved to be very incomplete, so that the present account is based entirely on a study of inseminated eggs. However, it is highly probable that maturation is identical in the two types of eggs of *Paracopidosomopsis*, as Silvestri ('06) has found to be the case in *Litomastix*.

It is not a difficult matter to obtain material for the study of maturation. The best way is to place a few non-parasitized moth eggs in a closed vessel containing a large number of female parasites. In the course of an hour each host will have deposited in it several eggs of the parasite—sometimes as many as twenty-five or thirty. The host eggs, thus serving as containers for the parasite eggs, can then be fixed as desired. No difficulty has

¹ Contribution from the Zoölogical Laboratory of the University of Texas, No. 132.

been experienced in cutting the moth eggs into sections from three to five microns thick. Preparations of the entire egg have also been used in the study of maturation. These were made from smears of the host egg.

THE FRESHLY DEPOSITED EGG.

The freshly laid egg of Paracopidosomopsis is a pear-shaped cell, very similar in appearance to that of Litomastix, as figured and described by Silvestri ('06). Different eggs vary considerably in size, and to some extent also in shape. In Fig. 2 is shown a typical egg some time after it had been deposited. The average egg measures about 115 μ in its long axis and 60 μ at its widest diameter.

The egg may be divided into two parts, the anterior portion or pointed end, and the posterior portion or broad end. At the time of deposition there is no line of demarcation between these two parts, but after the beginning of cleavage they are recognized as the polar region containing the polar nuclei, and the embryonal region consisting of the true embryonic cells.

The egg is surrounded by a thin but tough membrane, probably a true chorion. It is also possible that a very delicate vitelline membrane is present, although this is difficult of demonstration.

The contents of the egg consists of a very finely granular protoplasm in which are found a few scattered yolk or oil spherules (Fig. 8). The fertilized egg contains three distinct bodies, the germinal vesicle, the so-called nucleolus, and the sperm (Fig. 1).

The germinal vesicle is a very conspicuous spherical body, mesuring about 19 μ in diameter. Its chromatin is in the form of small stellate bodies. There is also present a small but distinct nucleolar-like body (Fig. 1, n). Although the position of the nucleus, as well as that of the nucleolus and of the sperm, is very variable, yet it usually lies toward the pointed end of the cell.

The so-called nucleolus in the eggs of polyembryonic insects has given rise to a great deal of discussion as to its origin and fate. Silvestri ('06, '08), who first described and named this body, thought that it arose at an early stage of the oöcyte from the germinal vesicle, but Martin ('14) and Hegner ('14, '15)

have demonstrated that it arises outside the germinal vesicle, and therefore does not represent a true nucleolus. Silvestri ('14) has later admitted the correctness of their conclusions, and proposed the term "oösoma." As to the fate of this body, Silvestri showed that it enters into certain definite cleavage cells, which he believed give rise to germ cells. Hegner has elaborated this idea, bringing it into harmony with his well-known views on germ-line-determinants.

The sperm is invariably found in the posterior half of the egg (Figs. I, 2, 8), indicating that insemination must take place at any point on the surface of the broad end of the egg. The entire sperm enters the egg (Fig. 8), and soon thereafter forms a small male pronucleus (Figs. I, 2, 13). There is no evidence that polyspermy ever occurs in the egg of this species, as no egg has ever been found with more than a single sperm in it.

FIRST MATURATION.

As in the eggs of many other Hymenoptera, the maturation divisions of *Paracopidosomopsis* do not result in the formation of distinct polar bodies, but instead only the chromatin undergoes division. Preparation for the first maturation division is seen in the appearance of heterotypic or bivalent chromosomes in the early prophase stage. These are sometimes in the form of V's and crosses, and in the clearest cases eight are present (Fig. 7).

The position of the first maturation spindle is very constant. It lies well toward the anterior end of the cell, with its long axis directed toward the center of the egg (Fig. 8). In the anaphase stage there is present a distinct mid-body at the equator of the interzonal or spindle fibers (Figs. 8, 9). At the close of the division the two groups of chromosomes are not reorganized into nuclei; but lie close together surrounded by clear spaces in the cytoplasm.

In only a few cases have I been able to determine accurately the number of chromosomes that pass to either end of the first maturation spindle. In Fig. 9 the outer, or first polar body group contains eight chromosomes, and at the lower end at least seven can be counted. In Fig. 10 the lower or second oöcyte group has eight clear chromosomes. In the upper or first polar body group eight are also present, but they are somewhat massed together. These observations indicate that the first maturation division results in separating the two components of each bivalent chromosome, so that the first polar body receives eight whole chromosomes, as does likewise the second oocyte.

SECOND MATURATION.

The second maturation occurs soon after the first is completed. The chromatin does not reorganize a nucleus. The first polar body chromatin likewise divides without forming a nucleus.

The second maturation and the division of the polar body may occur simultaneously (Fig. 12), or the polar body division may either precede (Fig. 11) or follow (Fig. 2) the second maturation division. There is therefore no close correlation between the divisions of these two groups of chromosomes.

In Fig. 11 the late anaphase stage of the first polar body division shows eight chromosomes at each end of the spindle. The group of chromosomes lying just below also has eight. This is the second oöcyte group. In Fig. 12 the two division figures are in the late anaphase stage. At the upper end of the polar body spindle (above) six chromatin masses are present, while at the lower end there are eight. The second oöcyte spindle has seven above and eight below. If these two divisions are equational in character, we should expect to find eight chromosomes in each group. Our failure to do so is probably due to the fact that one or more chromosomes in a group may be hidden by some of the other chromosomes.

FERTILIZATION.

As already stated the egg is inseminated by a single sperm, which lies in the lower half of the newly laid egg. Although the entire sperm enters the egg, only the sperm head becomes transformed into the male pronucleus, the formation of which is completed by the close of maturation.

Of the four groups of chromosomes referred to in connection with Fig. 12, the three lying nearest to the surface of the egg represent the three polar bodies, while the one lying toward the

center is the oötid group. The fate of the polar bodies will be considered later. The oötid group soon forms a small, condensed female pronucleus, which approaches the male pronucleus with which it eventually fuses. The pronuclei come together in the lower half of the egg. Apparently for a considerable period they lie close together before the actual fusion occurs. In Fig. 13 the two condensed pronuclei lie a short distance apart, with a small aster and its tiny centrosome lying between them. This case is interesting because it is the only one in which I have observed either a centrosome or aster in the eggs of this species.

The pronuclei remain apart while they undergo expansion, the female nucleus always being somewhat larger than the male nucleus (Fig. 15). Upon coming in contact with each other, the pronuclei fuse (Fig. 14) to form a single large conjugated, or cleavage nucleus (Fig. 16). Many different stages of conjugating nuclei have been observed in the preparations, one slide alone showing more than a dozen cases.

Discussion.

These observations show that in the egg of *Paracopidosomopsis* two typical maturation divisions occur, resulting in reducing the sixteen chromosomes of the primary oöcyte to eight in the oötid. It was shown in the second paper of the series that the sperm also receives eight chromosomes. The fertilized egg should therefore have sixteen chromosomes. A study of cleavage divisions shows that this is the case. Fig. 17 is a polar view of a metaphase plate of the first cleavage spindle. It has sixteen chromosomes. In Fig. 18 a side view of an anaphase stage is shown. This is one of the first four blastomeres undergoing division. There are fifteen chromosomes lying toward each end of the spindle, and the sixteenth, just completing its division, lies at the middle of the spindle, on the right.

A study of somatic cells shows that the diploid number of chromosomes is also present in them. Thus the dividing cells of the central nervous system of female larvæ have sixteen chromosomes (Figs. 3, 4). On the other hand, dividing cells from the central nervous system of male larvæ have but eight chromosomes (Figs.

5, 6). This is what would be expected, if males develop parthenogenetically from eggs that have undergone maturation.

AUSTIN, TEXAS,

March 5, 1917.

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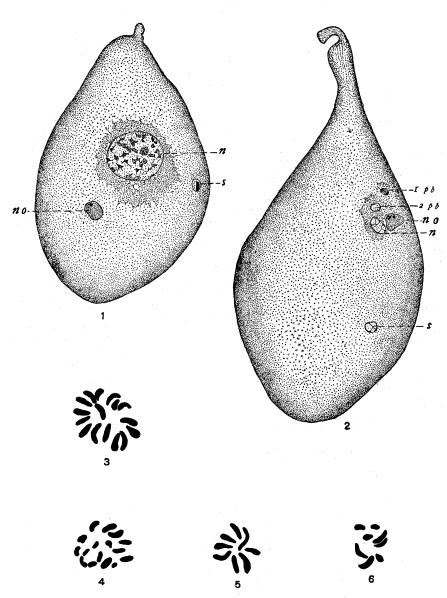
Silvestri, F.

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DESCRIPTION OF FIGURES.

PLATE I.

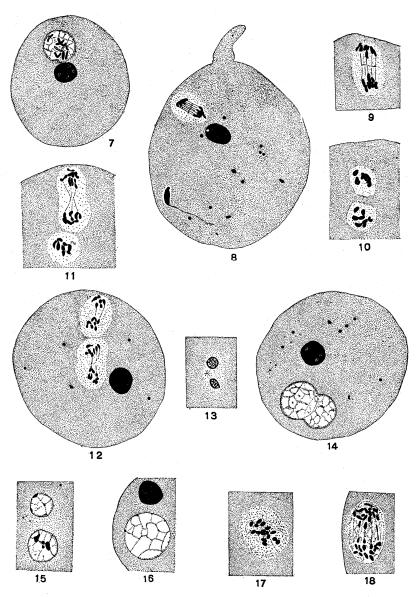
- Fig. 1. Entire egg from a smear preparation, made 23 minutes after oviposition. It shows the germinal vesicle (n), the sperm (s) and the nucleolus (no). $\times 720$.
- FIG. 2. Entire egg from a smear preparation, showing sperm (s), 1st polar body undergoing division $(1 \ p.b.)$, second polar body $(2 \ p.b.)$, egg nucleus (n), and nucleolus (n0). $\times 737$.
- Fig. 3. Metaphase plate of dividing cell from central nervous system of female larva. It shows 16 chromosomes. $\times 3857$.
 - Fig. 4. Same as 3. ×3857.
- Fig. 5. Metaphase plate of dividing cell from central nervous system of male larva. It shows 8 chromosomes. $\times 3857$.
 - Fig. 6. Same as 5. X3857.



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PLATE II.

- Fig. 7. Early prophase of first maturation. The black body close to germinal vesicle is the nucleolus. $\times 1,240$.
- FIG. 8. Late anaphase of first maturation. The sperm was drawn in from the next section to the left in the series. X1,240.
 - Fig. 9. First maturation spindle. X1,827.
- FIG. 10. First polar body chromosomes above, and chromosomes of the second oöcyte below. X1,827.
- FIG. 11. Anaphase stage of first polar body above, and chromosomes of second occyte below. X1,827.
- Fig. 12. Anaphase stages of the first polar body above, and second maturation below. $\times 1.240$.
- Fig. 13. Very early stage of the pronuclei, female above, male below. Note tiny aster lying between them. X1,240.
 - Fig. 14. Fusion of male and female pronuclei. X1,240.
 - Fig. 15. Pronuclei, male above, female below. X1,240.
 - Fig. 16. Conjugated nucleus. X1,240.
- Fig. 17. Polar view of first cleavage spindle, showing sixteen chromosomes. X1,827.
- FIG. 18. Side view of cleavage spindle of one of the first four cells. There are fifteen chromosomes in each daughter group. The sixteenth chromosome, which has just divided, lies on right side of spindle. ×1,827.



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